BEHAVIOURAL EFFECTS OF TEMPERATURE ON INSECTS

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Like the propagation of light rays, radiation of heat occurs in straight rays consisting of waves. The wave length and the amount of energy determine the intensity of heat or temperature, which is readily measurable. Heat is due to infra rays ranging from 0.1 mm to 770 mμ and decreases towards the visible spectrum. Temperature is a physical factor as well as a stimulus for insects. It can be a token stimulus or a sign for some other thing as in the case of insect parasites of vertebrates.

Life is limited within a range of temperature at the limits of which survival depends upon certain physiological adaptations in poikilothermic animals, such as selection of preferred temperature, variation in water distribution, regulation of water loss, and other metabolic reactions including suspension of active life processes at unfavourable temperatures (Prosser, 1952). Heat may be lost by radiation, convection, conduction, vaporization of water, and circulation of heat from interior to surface, while gain of heat occurs by absorption of heat largely from the solar radiation, besides oxidative and other metabolic means.

COLD AND HEAT RECEPTORS

The mechanism of temperature perception is not known and there is no indication of an "intermediate substance" being involved between the sensory receptor cell and the heat waves. Anatomically the temperature sense organs are simple sensory cells and are usually localized by observation of the reactions of insects to temperature and the way their behaviour modifies on amputation of various parts of insect body. Temperature receptors can now be studied electrophysiologically (table 1).

Wigglesworth and Gillett (1934) suspect their type iii sensilla on upper two third area of the first flagellar segment and entire second (=last) flagellar segment as the heat receptors since they are the most numerous in distribution. They are fine, curved, small, slender structures ending in a sharp point. Histologically the sensillum is thick-walled, with a very small central cavity and a small gland cell having five or six nerve cells. Slifer (1951, 1953) has found that the males of the African migratory locust have the largest heat sensitive areas on fourth, fifth, and sixth abdominal terga and suggests that these may serve to protect the spermatozoa from excessive heat, because they are located just above the gonads. Similarly fenestrae may be used by the female in finding a suitable temperature for oviposition.

Not much work has been done on the electrophysiology of temperature receptors. Hodgson and Roeder (1956) showed a positive temperature effect for the sensory discharges of taste-receptors in *Phormia*. Kerkut et al. (1957) for the first time found evidence for cold receptors in insects by studying the electrical responses of the isolated limb of the American cockroach following localized warming and cooling. The receptors are sensitive to 1° C drop in temperature of the substratum with which the feet of the cockroach are in contact over the critical range below 13° C, but are less sensitive to a rise of temperature, being stimulated by 5° C rise. This is like the increased activity of cold receptors in cat's tongue at low temperature (Dodt et al., 1952).

Thermoreception occurs by lateral line organs in fishes (Rubin, 1935), ampullae of Lorenzini in elasmobranchs (Sand, 1938), dermal receptors in general (Dijkgraaf, 1943; Hesse, 1924), heat and cold dermal receptors in frog (Morgan, 1922), sensory pits in pit vipers and head of certain boas (Noble et al., 1937), Ruffini organs which lie deeper in integument and the cold receptors, bulbs of Krouse located peripherally in man (Bazett, 1941; Bazett et al., 1930).

EFFECT OF RADIATION ON BODY TEMPERATURE

Insects in general are poikilotherms, but some of them exhibit a limited degree of heterothermy by maintaining their body temperature a little higher or lower than that of their environment. Examples are *Vanessa* butterfly and certain lamellicorn beetles that "warm up" before "take off" in air (Dotterweich, 1928; Krogh et al., 1941; and Oosthuizen, 1939); honeybees during summer and winter periods decrease and increase the colony temperature accordingly (Himmer, 1932 and Pirsch, 1923); the grasshopper, *Oedipoda coerulescens*, gets warmer than air shortly after sunset (Franz, 1930); and *Schistocerca gregaria* has its body temperature fluctuating between 40° and 45° C during the day, a little higher than the air (Bodenheimer, 1930).

TABLE 1
Cold and heat receptors

Arthropod	Location of sense organs	Remarks	Reference
Crickets	antennae, cerci and mouth parts, tarsi		Herter, 1923
Blabera fusca	labial palps, tarsi	by hot needle	Herter, 1924
Liogryllus campestris	antennae, labial palp, tarsi, cerci	same	Herter, 1924
Melanoplus differentialis, *M. femur-rubrum* and *Disossteria carolina*	antennae, pulvilli, tarsi, dorsal and ventral sides of abdomen and palps	increasing order of sensitivity	Geist, 1928
Collembola	antennae		Strebel, 1932
Menexenus semiarmatus	12th antennal segment, dorsal surface	by ampuattion	Cappe de Baillon, 1932
Rhodnius prolixus	1st and 2nd flagellar segments of antenna	type iii in their fig.	Wigglesworth et al., 1934
Carausius morosus	14th antennal segment	by amputation	Herter, 1939
Ixodes reduvius	on leg and body surface		Lees, 1948
Dorcus parallelepipideus	three distal antennal segments, maxillary palpi		Gebhardt, 1951 and 1953
Otiorrhynchus ligustici	antennae, tarsi		ibid.
Pyrrhocoris apterus, *Lygaeus equestris*	antennae		ibid.
Locusta migratoria migratoriodes	antennal crescents and fenestrae	by histology, hot glass rod	Slifer, 1951 and 1953
Periplaneta americana	hairs on tarsi, arolium and pulvilli	cold receptor	Kerkut et al., 1957
Opisthothalmus latimanus	abdomen	for thermo-regulation	Alexander et al., 1958

It is thought that coloration plays some role in the thermal economy of insects (Schröder, 1903), but others like Szilady (1921) and Lengerken (1924–27) maintain that metallic colors in insects, like beetles, serve to reflect heat rays in sunshine. Krüger (1929) showed that the wings considerably reflect heat rays while the general body of the butterfly, *Parnassius apollo* absorbs them. According to Huard et al. (1951) however, the primary function of the wing spots is absorption of heat rays. Of the grasshopper, *Kripa coelevriensis*, the blackish-brown form maintained at a 4 to 5° C higher temperature than the buff-colored forms, when both were equally exposed to the sun (Buxton, 1924). Solar radiation alters the body temperature of the desert locust, *Schistocerca gregaria*, which is regulated by change in posture (Fraenkel, 1929 and 1930). Thus, they show no signs of activity below 17° C, move around at 17 to 20° C, and assume such a posture as to receive maximum solar radiation on their perpendicularly oriented bodies. They move about from 30° C upwards to 40° C, when they orient their posture parallel to the sun's rays, thereby receiving minimum solar radiation.

Animals, like lizards and snakes, also form basking groups with respect to solar radiation with the result that, for instance, certain desert lizards have a cloacal

temperature of 38° C at an air temperature of 13° C (Cowles, 1947). While receiving maximum radiation they expand their chromatophores, but are constricted after an optimum body temperature is attained (Gunn, 1942). The lodgepole needle miner, *Recurvaria milleri*, is prevented from over-heating by the orientation of the needles other than 90° to the sun's rays (Henson et al., 1952).

TEMPERATURE PREFERENDUM

Behavioural regulation of body temperature occurs by selection of preferred temperature in nature as well as in the laboratory in an apparatus with a whole series of temperature gradients, where light, humidity, and internal factors such as hunger and sexual activity are controlled (Fraenkel et al., 1940). The preferred temperature region is known by many names such as vorzugstemperatur, thermal or temperature preferendum, temperature optimum, and eccritic temperature (Herter, 1926, 1932; Bodenheimer et al., 1928; Gunn et al., 1938). Some of these terminologies, however, carry anthropomorphic implications, and this criticism is true not only for this, but for much of the studies in insect behaviour. High temperatures cause a direct metabolic effect on the organism resulting in greater speed of locomotion, and an indirect effect of avoiding reactions by action through the nervous system, which no longer exists under optimal conditions.

Cockroaches and other insects are known to prefer warm places. Whereas, cockroaches are active in night, they exhibit what may be taken as an indication of orthokinetic reaction to temperature during daytime as the speed of running increases in warmer regions until it is brought back into the preferendum (Gunn, 1934). The blowfly, *Lucilia cuprina*, has a peak of 33 percent activity at 20° C, another peak of 6 percent activity at 42° C, and is immobile at 5° C (Nicholson, 1934). Subterranean larvae move vertically in soil, probably with regard to temperature, e.g., larvae of *Polyphylla oliveri* (Prinz, 1928) and *Malacosoma* caterpillars (Howlett, 1910).

Temperature preferendum values obtained in laboratory experiments for insects are generally related to the temperatures of their environments. In nature, *Fannia canicularis* emerges earlier in the year than *Musca domestica*, and in laboratory the former is active between 9° C and 35° C, while the latter is active between 14° C and 43° C. The maximum activity occurs at 21° C and 40° C, respectively (Nicholson, 1934). The preferred temperature for *Haematopinus suis* is 28.6° C (Weber, 1929).

The preferred temperature of an insect may vary during its life history. Thus in the housefly, migration from the feeding place (=dung) to pupation site (=ground) is due to behavioural changes in the central nervous system which modifies the temperature preferendum as the larvae grows. The optimum temperature during active feeding is 30° C to 34° C and drops to 17° C when ready for pupation (Thomson et al., 1937). Diurnal activity seems to be controlled by air temperature in slugs, where Dainton (1954) recorded activity between 4° C and 20° C and sensitivity to minute temperature changes such as 0.1° C in an hour. *Paramaecium*, among protozoans, also exhibits selection of preferred temperature (Mendelssohn, 1815; Loeb, 1918).

ORIENTATION IN PARASITIC ARTHROPODS

Temperature is a token stimulus for ectoparasitic arthropods which serves to lead them to their hosts by the warmth of their body. Temperature helps in securing bloodmeal for them, which they are really looking for, and not just heat. If already fed, the same insects may not exhibit any response to temperature stimulus. This response under favorable circumstances is directly proportional to the positive differential temperature of the surface between host body and environment.

Howlett (1910) showed that females of *Culex fatigans* and *Stegomyia scutellaris* may be attracted to a tube of hot water but not at all to isolated blood or human

sweat, and the males show no such reactions at all. Females of *Anopheles punctipennis*, and to a lesser extent males, also are similarly attracted to an empty heated glass plate and the former may even attack the surface with their proboscis (Marchand, 1918). This response is absent among the hibernating females of *Culex* and the wingless hoglice, *Haematopinus suis*, which obviously cannot move around to find the host by warmth and lives permanently on its host (Marchand, 1920). Temperature sensitive areas occur on the antennae of the bedbug, *Cimex lectularius* (Rivnay, 1932; Sioli, 1937). Radiant heat initiates a reaction of "hesitation in walking" and host-finding reaction is by trial and error and could be termed as a klinotactic orientation.

Wigglesworth and Gillett (1934) have studied in detail the orientation to radiant heat of the South American blood-sucking bug, *Rhodnius prolixus*. Blinded insects went straight to a test tube of warm water from a distance of 3 to 5 cm; thus vision is not involved and heat of the tube could be the only possible stimulus. The reactions disappeared on extirpation of both antennae, but not one. The bug responds to the gradient of air temperature around the source of stimulus. The receptors on the antennae perceive the gradient up an antenna when it is held along the gradient, and by moving their antennae and comparing the heat intensity which is successive in time, the insects move towards the direction of heat source. Such a movement is klinotaxis (Fraenkel et al., 1940) and not tropotaxis, since the result of unilateral removal of receptor is not circus movement, but there is a slight tendency to turn towards the intact side, which may suggest the involvement of a tropotactic element. That this is not the case may be explained by the fact that the centers of the two heat sources were 5.5 cm apart and the bugs were left 3 to 4 cm away from each source. This distance is very small and corresponds to that part of the gradient where it is hard to differentiate between klinotactic and tropotactic orientation. Theoretically, a slight deviation in a small insect on any side would yield different results. The "reflex pursuit of the antennae into the region of optimal stimulation" thus corresponds to klinotaxis and not to tropo- or telo-taxes.

Homp (1938), working with the louse, *Pediculus vestimenti*, found that its temperature preferendum was between 25 and 33° C, with a peak at about 29° C, when placed in a concentric temperature gradient by means of an "artificial hot finger." The avoiding reactions have been termed "klino-taxis" by Fraenkel and Gunn (1940), because the path assumed by the lice was wavy, but directed towards the source of stimulation and not just random in direction. Perhaps the term, "thermo-meno-taxis" used by Homp, which is comparable to light compass reaction, is not accurate since the orientation is not necessarily at a fixed angle to the direction of temperature stimulus, and there is no reason to believe that lice do not react to radiant heat. The circular path of lice near the source of temperature simply means that they were in the zone of preferred temperature and were exhibiting random undirected locomotion, which is consistent with the term "klinokinesis." Unlike *Rhodinus*, *Pediculus* without antennae can still orientate. It crawls straight to a warm tube and follows it as the tube is displaced. With equal sources of heat, most of them move halfway between the two, while some crawl directly to one of them or in a parabola to one or the other.

Using a circular apparatus heated at the center, Totze (1933) showed that the tick, *Ixodes reduvius*, exhibited a klinokinetic reaction on approaching the preferendum. The ticks show avoiding reactions to high temperature, but do not move away from low temperature gradients (Lees, 1948). In a temperature organ, ticks turn abruptly on approaching the high temperature zone, move in a straight line and get slower as the temperature drops and collect at the cool end of the gradient. This locomotion away from the hot end of the temperature organ could be indicative of a negative telotaxis, but since the reaction is dependent upon intensity of heat and it is slow towards the cool end, it may better be considered an orthokinetic reaction. It is, however, quite possible that the increased

speed of locomotion at the higher temperature is a metabolic effect of temperature and not a behavioural effect through the central nervous system. A token stimuli of warmth and odor of sheep wool both are involved in the host-finding reaction of the sheeptick, *Ixodes reduvius*.

Temperature is a token stimulus for the medicinal leech, *Hirudo medicinalis* between 33 to 35° C, which is close to the host's temperature (34.4° C), and they suck to a hot tube, but stop at 39° C and leave at 41.5° C (Herter, 1929). Similarly *Glossiphonia complanata*, an invertebrate parasite, comes to a tube at 26° C, and the fish leech, *Hemiclepsis* at 31° C (Herter, 1928).

ORIENTATION OF LOCUSTS TO RADIANT HEAT

The gregarious hoppers of the locust, *Locusta migratoria migratorioides*, have a fairly definite daily routine of behaviour. Chapman (1955) writes, "At night they are quiescent on plants (=roosting). At dawn they become active and ascend higher up the stems. Feeding follows until, when the morning is well advanced, the hoppers descend from the plants and soon form basking groups. Depending on conditions, the basking group persists or the hoppers start to march. If marching occurs, it stops as evening approaches and basking groups are formed again. These later break up and the hoppers ascend to the night roosting positions, feeding until the temperature becomes too low." The sense organs involved in temperature perception have already been mentioned (table 1) and the following account is a critical review and analysis of the various movements in locusts in relation to solar radiation. The behaviour of locusts can be conveniently described under the following divisions: first movements, morning ascent and exposure to sun, morning descent, and evening ascent.

First movements.—The first movement is awakening with the sunrise, and two factors can operate in the field, light intensity and temperature, which are rapidly changing at this time, but humidity is also possible as a third factor. At 15° C cold stupor occurs in *Locusta* (Hussein, 1937) so that insects that often do not move until after sunrise are able to exhibit responses to light, but can not do so because of the low temperature. Chapman (1955) found that below 20° C restricted movements can occur, so photokinesis is not considered as a major factor. The major factor in awakening is positive thermokinesis, with photokinesis playing a minor role.

Morning ascent and exposure to sun.—As the temperature rises, a negative response to gravity occurs which is the main cause of the ascent (Lepiney, 1933; Kennedy, 1939; Regnier, 1931; and Chapman, 1955). There is no indication in laboratory tests that hoppers can move along a temperature gradient, and we also know that below 15° C cold stupor onsets, so the only role of temperature in morning ascent could be one of increasing the metabolic activity. Morning ascent results in exposure to radiant heat, and this is a transient period since very soon the heated hoppers begin to descend.

Morning descent.—It is a well-known phenomenon that as the sun rises high the hoppers descend from their host plants. There are two factors involved in the field during morning descent, the actual downward movement or descent of the hoppers, and another factor, of suitable ground temperature for basking which prevents hoppers from reascending after descent and is responsible for vacation of the roosting sites. There are reasons to believe that it is not just a matter of chance or due to negative phototaxis (Kennedy, 1939) or change in relative humidity (Zolotarevsky, 1933), but a thermotactic response (Fraenkel in Bodenheimer, 1929).

It has been shown in laboratory experiments that an inverted air temperature gradient plays no part in morning descent (Chapman, 1955). Husain (1932) found no descent in *Schistocerca* even at 45° C when the temperature conditions were uniform, indicating that it is very necessary for the ground temperature to exceed air temperature if the roosts are to be vacated. Similar results are

obtained by Rubtzov (1935), Strelnikov (1936), and Kennedy (1939). Air movement affects mechanically, or by causing a fall in body temperature, thus resulting in increased activity and descent.

Evening ascent.—In the evening the hoppers leave their basking groups and ascend on the surrounding vegetations. This phenomenon roughly coincides with sunset and when the ground is cooled. Ascent occurs in *Locusta migratoria migratorioides* two hours before sunset (Shumakov, 1940), not until sunset if ground temperature does not fall earlier in *L. migratoria capita* (Zolotarevsky, 1930), and about half an hour before sunset in *Schistocerca* (Regnier, 1931).

No evidence was obtained in laboratory tests for a role of positive phototaxis in the evening ascent (Chapman, 1955), although some people suggest it to be the case in field (Allan, 1933; Kennedy, 1939; Kiritchenko, 1926; Pielou, 1948; and Telenga, 1930). The ascent can not be considered as due to an inherent tendency on the part of the locust to sit head upwards in a vertical position as has been suggested by Williams (1933), since there is tremendous variation in posture of sitting. The works of Burnett (1951), Fraenkel (1929), Kennedy (1939), Pielou (1948), and Regnier (1931) all point at the importance of negative geotaxis in the evening ascent.

Under laboratory conditions, Chapman (1955) found that hoppers did not start to ascend until the ground temperature dropped, and until the activity of the hoppers was such that they ceased to bask, but there was a tendency to stay up after once ascending on roosting sites. The roosting position was disturbed by increased air temperature since the hoppers became highly active and could not maintain their position. Recent feeding inhibited this activity. It is possible for the hoppers to follow the sun up as a temperature response, but body temperature is not found to be a factor in evening ascent.

It could be concluded from these observations that the behaviour of locusts is mostly random, undirected, and kinetic, while upward climbing and roosting following the evening ascent may be directed and taxic. Of all the internal and external factors modifying their behaviour, radiant heat appears to be by far the most important, especially in orientation to solar radiation.

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LITERATURE CITED

Alexander, A. J., and **D. W. Ewer.** 1958. Temperature adaptive behaviour in the scorpion, *Opisthothalmus latimanus*. J. Exptl. Biol. 35: 349–359.

Allan, W. 1933. The movement and breeding of locust swarm (July 1931-Sept. 1932). Ann. Bull. Dept. Agr. N. Rhod. 2: 25–34.

Bazett, H. C., B. McGlone, and **R. J. Brocklehurst.** 1930. Stimulation of cutaneous thermoreceptors in man. J. Physiol. 69: 88–112.

Bazett, H. C. 1941. In Temperature, Its Measurement and Control in Science and Industry. Reinhold, New York. pp. 489–501.

Bodenheimer, F. S., and **D. Schenkin.** 1928. Die temperatur abhängigkeiten einiger Insekten. Zeit. f. vergl. Physiol. 8: 1–15.

———. 1930. Studien zur Epidemiologie, Ökologie und Physiologie der afrikanischen wanderheuschrecke (*Schistocerca gregaria*, Forsk.). Zeit. angew. Entomol. 15: 1–123.

Burnett, G. F. 1951. Field observations on the behaviour of the red locust (*Nomadacris septemfasciata* Serville) in the solitary phase. Anti-Locust Bull., London. no. 8, 36 pp.

Buxton, P. A. 1924. Heat, moisture and animal life in deserts. Proc. Roy. Soc. Lond. (B) 96: 123–131.

Cappe de Baillon, P. 1932. La sensibilite thermique des Phasmidae. Compt. Rend. Acad. Sci. Paris 195 (3): 557–559.

Chapman, R. F. 1955. Some temperature responses of nymphs of *Locusta migratoria migratorioides* (R.&F.), wiht special reference to aggregation. J. Exptl. Biol. 32: 126–139.

———. 1955. A laboratory study of roosting behaviour in hoppers of the African Migratory Locust (*Locusta migratoria migratorioides* R. & F.). Anti-Locust Bull., London. no. 19, 40 pp.

Cowles, R. B. 1947. Comments by readers. Science 105: 282.
Dainton, B. H. 1954. The activity of slugs. J. Exptl. Biol. 31: 165–197.
Dijkgraaf, S. 1943. Temperature sense in fish. Zeit. f. vergl. Physiol. 30: 252.
Dodt, E., and **Y. Zotterman.** 1952. The discharge of specific cold fibres at high temperatures. Acta Physiol. Scand. 26: 358–365.
Dotterweich, H. 1928. Beiträge zur Nervenphysiologie der Insekten. Zool. Jahrb. Abt. allg. f. Zool. u. Physiol. 44: 399–450.
Fraenkel, G. 1929. Untersuchungen über Lebensgewohnheiten, Sinnesphysiologie und Sozialpsychologie der wandernden Larven der afrikanischen Wanderheuschrecke *Schistocerca gregaria* (Forsk.). Biol. Zentralbl. 49: 657–680.
———. 1930. Die Orientierung von *Schistocerca gregaria* zu strahlender Wärme. Zeit. f. vergl. Physiol. 13: 300–313.
——— and **L. D. Gunn.** 1940. The Orientation of Animals. Oxford. 318 pp.
Franz, H. 1930. Untersuchungen über den Wärmehaushalt der Poikilothermen. Biol. Zentralbl. 50: 158–182.
Gebhardt, H. 1951. Lokalisatorischer Nachweis von Thermorezeptoren bei *Dorcus parallelepipedus* L. und *Pyrrhocoris apterus* L. Experientia, Basle, 7: 302–303.
———. 1953. Die Lage de wichstigsten Thermorezeptoren bei einigen Insekten. Zool. Jb. Jena (Allg. Zool.) 63: 558–592.
Geist, R. M. 1928. The heat sensitive areas of certain grasshoppers. Ann. Entomol. Soc. Am. 21: 614–618.
Gunn, D. L. 1934. Temperature and humidity relations of the cockroach. II. Temperature preference. Zeit. f. vergl. Physiol. 20: 617–625.
——— and **C. A. Cosway.** 1938. Humidity preference of *Blatta orientalis*. J. Exptl. Biol. 13: 450–459.
———. 1942. Body temperature in poikilothermal animals. Biol. Rev. 17: 293–314.
Henson, W. R., and **R. F. Shepard.** 1952. The effects of radiation on the habitat temperatures of the lodgepole needle miner, *Recurvaria milleri* Busck. (Gelechidae: Lepidoptera). Canad. J. Zool. 30: 144–153.
Herter, K. 1923. Temperatursinn der Hausgrille (*Acheta domestica*) und der roten Waldameise (*Formica rufa*). Biol. Zentralbl. 43: 282–285.
———. 1924. Temperatursinn einiger Insekten. Zeit. f. vergl. Physiol. I: 221–288.
———. 1926. Thermotaxis und Hydrotaxis bei Tieren. Bethes Handb. norm. path. Physiol. II: 173–180.
———. 1928. Reizphysiologie und Wirtsfindung des Fischegels, *Hemiclepsis marginata*. Zeit. f. vergl. Physiol. 8: 391–444.
———. 1929. Reizphysiologisches Verhalten und Parasitismus des Entenegels, *Protoclepsis tesselata*. Zeit. f. vergl. Physiol. 10: 272–308.
———. 1932. Nachträge zu Herter, 1926. Bethes Handb. norm. path. Physiol. 18: 280–282.
———. 1939. Über den Temperatursinn der Insekten. In 7 int. congr. Entomol. 2: 740–759.
Hesse, R. 1924. Tiergeographie auf Ökologischer Grundlage. Jena, Fischer. pp. 164–165.
Himmer, A. 1932. Dei temperaturverhältnisse beiden Sozialen Hymenopteren. Biol. Rev. 7: 224–253.
Hodgson, E. S., and **K. D. Roeder.** 1956. Electrophysiological studies of arthropod chemoreception. I. General properties of labellar chemoreceptors in diptera. J. Cell. Comp. Physiol. 48: 51–76.
Homp, R. 1938. Wärmeorientierung von *Pediculus vestimenti*. Zeit. f. vergl. Physiol. 26: 1–34.
Howlett, F. M. 1910. The influence of temperature upon the biting of mosquitoes. Parasitology 3: 479–484.
Huard, G., and **R. P. Corbe.** 1951. Recherches photometriques sur *Parnassius apollo* L. (Lepidopteres). Bull. Soc. Zool. France 76: 18–21.
Husain, M. A. 1932. Report of the locust research entomologist at Lyallpur, West Pakistan. ii+105 pp. (unpublished).
Hussein, M. 1937. The effect of temperature on locust activity. Bull. Minist. Agr. Egypt, Cairo. no. 184, 55 pp.
Kennedy, J. S. 1939. The behaviour of the desert locust (*Schistocerca gregaria* Forsk.) (Orthoptera) in an outbreak centre. Trans. Roy. Entomol. Soc. Lond. 89: 385–542.
Kerkut, G. A., and **B. J. R. Taylor.** 1957. A temperature receptor in the tarsus of the cockroach, *Periplaneta americana*. J. Exptl. Biol. 34: 486–493.
Kiritchenko, A. 1926. Materials for the ecology and bionomics of *Calliptamus italicus*, L., in the steppe zone of Ukraine. Odes'ka Reg. Agr. Exp. Sta., Entomol. Dept. I: 47 pp. (In Russian).
Krogh, A., and **E. Zenthen.** 1941. The mechanism of flight preparation in some insects. J. Exptl. Biol. 18: 1–10.
Krüger, P. 1929. Über die Bedeutung der ultraroten Strahlen für den Wärmehaushalt der Poikilothermen. Biol. Zentralbl. 49: 65–82.
Lees, A. D. 1948. The sensory physiology of the sheep tick, *Ixodes ricinus*. J. Exptl. Biol. 25: 145–207.

Lengerken, H. von. 1924–27. Coleoptera. Käfer. P. Schulze, Biologie Tiere Deutschlands, Berlin (Lfg. 10, 12, 16, 24), Teil 40: 1–346.
Lepiney, J. de. 1933. Revision sommaire du comportement de *Schistocerca gregaria* Forsk., ph. *gregaria*, dans les lieux d'habitat temporaire. In 5 int. congr. Ent., Paris (1932): 573–584.
Loeb, J. 1918. Forced Movements, Tropisms and Animal Conduct. J. B. Lippincott Co., Philadelphia. pp. 155.
Marchand, W. 1918. First account of a thermotropism in *Anopheles punctipennis*, with bionomic observations. Psyche 25: 130–135.
———. 1920. Thermotropism in insects. Entomol. News. 31: 159–165.
Mendelssohn, M. 1895. Über den Thermotropismuseinzelliger Organismen. Arch. ges. Physiol. 60: 1–27.
Morgan, A. H. 1922. The temperature senses in the frog's skin. J. Exptl. Zool. 35: 83–114.
Nicholson, A. J. 1934. Influence of temperature on the activity of sheep blowflies. Bull. Entomol. Res. 25: 85–99.
Noble, G. K., and **A. Schmidt.** 1937. The structure and function of the fascial and labial pits of snakes. Proc. Am. Phil. Soc. 77: 263–288.
Oosthuizen, M. J. 1939. Muscle temperature before and during flight in insects. J. Entomol. Soc. S. Africa 2: 63–73.
Pielou, D. P. 1948. Observations on the behaviour of gregarious hoppers of the red locust, *Nomadacris septemfasciata* Serville. Proc. Roy. Entomol. Soc. Lond. (A) 23: 19–27.
Pirsch, G. B. 1923. Studies on the temperature of individual insects, with special reference to the honeybee. J. Agr. Res. 24: 275–288.
Prinz, I. Y. 1928. On the pests of the vine. Entomol. Cab. Agr., Co-oper. Soc. Concordia, Tiflis, 2: 127 pp. (In Russian).
Prosser, C. L. 1952. Comp. Animal Physiol. Saunders Co., Philadelphia. p. 374.
Regnier, P. P. 1931. Les acridiens ravageurs du Maroc. Rabat, Dir. gen. Agr. Comm. et Colon., Def. cultures, 41 pp. (2nd edition).
Rivnay, E. 1932. The tropisms of the bedbug, *Cimex lectularius*. Parasitology 24: 121–136.
Rubin, M. A. 1935. Thermal reception in fishes. J. Gen. Physiol. 18: 643–647.
Rubtzov, I. A. 1935. Regularities in the development and behaviour of Siberian Acrididae in connection with climatic factors. Bull. Acad. Sci. U.R.S.S., Leningrad 1935: 789–824. (In Russian with German summary).
Sand, A. 1938. The function of the ampullae of Lorenzini, with some observations on the effect of temperature on sensory rhythms. Proc. Soc. Lond. (B) 125: 524–553.
Schroder, C. 1903. Kritik der von Herrn Dr. E. Fischer (Zürich) aus seinen "Lepidopterologischen Experimentalforschungen" gezogenen Schlüsse auf Grund einer enuen Erklärung des Wesens derselbent. Allg. Zeit. Entomol. 8: 437–447.
Shumakov, E. M. 1940. The cause of gregariousness in Acrididae. Proc. Lenin Acad. Agr. Sci., Leningrad. 21: 10–15 (In Russian).
Sioli, H. 1937. Thermataxis und Perzeption von Wärmestrahlen bei der Bettwanze, *Cimex lectularius*. Zool. Jahrb. Abt. allg. f. Zool. u. Physiol. 58: 284–296.
Slifer, E. H. 1951. Some unusual structures in *Locusta migratoria migratorioides* and their probable functions as thermoreceptors. Proc. Roy. Soc. (B) 138: 414–437.
———. 1953. The pattern of specialized heat sensitive areas on the surface of the body of Acrididae (Orthoptera). Trans. Am. Entomol. Soc. 79: 37–97.
Strebel, O. 1932. Beiträge zur Biologie, Ökologie und Physiologie einheimischer Collembolen. Zeit. f. Morphol. u. Ökol. Trere 25: 31–153.
Strel'nikov, I. D. 1936. Effect of solar radiation and microclimate upon the body temperature and behaviour of the larvae of *Locusta migratoria* L. Trav. Inst. Zool. Acad. Sci. U.R.S.S., Leningrad 2(1935): 637–733. (In Russian with English summary).
Szilady, Z. 1921. Thermoskopische Farben im Tierreich. Festschriftzum II. Ferienhochschulkurs, Nagy Szeben. pp. 65–84.
Telenga, N. A. 1930. Biological observations on *Schistocerca gregaria*, Forsk. in Kohresm in 1929. Izre, Khoresm sel-Khoz. Opuit., Moscow 6: 27 pp. (In Russian).
Thomson, E., and **M. Thomsen.** 1937. Über das Thermopräferendum der Larven einiger Fliegenarten. Zeit. f. vergl. Physiol. 24: 343–380.
Totze, R. 1933. Sinnesphysiologie der Zecken. Zeit. f. vergl. Physiol. 19: 110–161.
Weber, H. 1929. Biologische Untersuchungen an der Schweinlaus (*Haematopinus suis* L.) unter besonderer Berücksichtigung der Sinnesphysiologie. Zeit. f. vergl. Physiol. 9: 564–612.
Wigglesworth, V. B., and **J. D. Gillett.** 1934. The function of the antennae i ı *Rhodnius prolixus* (Hemiptera) and the mechanism of orientation to the host. J. Exptl. Biol. II: 120–139.
Williams, C. B. 1933. Observations on the desert locust in East Africa from July 1928 to April 1939. Ann. Appl. Biol. 20: 463–497.
Zolotarevsky, B. N. 1930. Le Criquet Migrateur (*Locusta migratoria* Sauss.) a Madagascar. Ann. Epiphyt., Paris 15 (1929): 185–236.
———. 1933. Contribution a l'etude biologique du Criquet Migrateur (*Locusta migratoria capito*, Sauss.) dans des foyer permanents. Ann. Epiphyt., Paris 19: 47–142.